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A BASAL NEW SPECIES OF *OLBIOGASTER* (DIPTERA: ANISOPODIDAE) IN DOMINICAN AMBER, AND ITS SYSTEMATIC PLACEMENT

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Abstract.—A distinctively new species of *Olbiogaster* is described from Oligo-Miocene amber of the Dominican Republic. It is based on a single, virtually complete female and named **Olbiogaster perezi**. Phylogenetic analysis of external morphological characters indicates it is probably the sister group to all of the living species of the genus, or at least among a group of phylogenetically basal species. The four living species of *Olbiogaster* described from Caribbean islands belong to clades that are more recently derived than is the fossil.

Key Words: Anisopodidae, amber, *Olbiogaster,* cladistics

The family Anisopodidae, in the broad sense, is a small family of relatively primitive flies that is of keen phylogenetic interest. Only about 100 species are described for the family, which is probably no more than half of the actual number of species. The larvae occur under bark of decaying trees, rotting vegetation, and associated with fungi. Major, synthetic papers on the systematics of the family are by Amorim and Tozoni (1994) and Tozoni (1989). The former is a phylogenetic classification of the world genera of Anisopodidae, s.l.; the latter is a phylogenetic study of the species of *Olbiogaster,* from which we drew heavily for characters to study.

This is the second paper on Dominican amber Anisopodidae. The first one, by Grimaldi (1991), described four species: *Valeseguya disjuncta, Mycetobia antillea, Mycetobia cryptambra,* and *Mesochria neotropica.* The last three species Amorim and Tozoni (1994) are placing in a new genus, *Neomesochria,* with all the Neotropical species formerly put into *Mycetobia* as well as two New Caledonian species. *Valeseguya disjuncta* is of great interest because it is a relict: its closest living relative is *Valeseguya rieki* from Australia, the only other member of this aberrant genus. Amorim and Tozoni (1994) placed *Valeseguya* in a narrowly defined family, the Mycetobiidae (including also *Mycetobia, Mesochria,* and *Neomesochria*). The placement of *Valeseguya* with mycetobiines is currently being tested using DNA sequences from the amber fossils (DeSalle and Grimaldi, in prep.). *Valeseguya disjuncta* is curiously much more common than the other mycetobiines in Dominican amber (even though the genus is now restricted to Australia). Also, the extinct species is represented by a large series of males and females; the one living in Australia is represented by a few poorly preserved males. The finding of an *Olbiogaster* in Dominican amber now adds a major new component to this extinct fauna of anisopodids.

METHODS AND MATERIALS

We are indebted to J. Manuel Perez for providing the specimen to us for study. Exact provenance within the Dominican Republic is uncertain but derives from the group of central mines in the mountains surrounding Santiago. Despite repeated citations of Dominican amber being Eocene in age (ca. 40 myo), there is very little basis for that dating. Grimaldi (1995) reviewed the stratigraphic evidence. At present it is most prudent to assume a Miocene-Oligocene age (ca. 25 million years old). The specimen was prepared and photographed as given in Grimaldi (1991, 1993).

SYSTEMATICS

Genus *Olbiogaster* Osten-Sacken, 1886

Tozoni (1989) and Amorim and Tozoni (1994) provided diagnostic characters of the genus. These included several aspects of male sternite 10 (bifid apically, with a pair of lateral projections, and slender at the base but apically enlarged) and the gonostyles (slender, with setae on the outer face). The most obvious feature that distinguishes this genus is vein M_3 weaker than the other posterior veins.

The genus *Olbiogaster* is restricted to the New World, with all but two species being Neotropical. Tozoni (1989) indicated that there were 7 undescribed species from Brazil. Only 4 species are described from the Caribbean: *antillarum* Lane & D'Andretta (U.S. Virgin Islands), *fulva* Edwards (Puerto Rico), *danista* Stone and *evansi* Stone (island of Dominica, Lesser Antilles).

Olbiogaster perezi Grimaldi and Amorim, NEW SPECIES

Fig. 1

Diagnosis.—Head and thorax with distinctive pattern of dark brown areas (see description). Wing with stigma surrounding basal half of vein R_{2+3}. Discal cell fusiform, ends not truncate, with medial veins branching directly off apical point. Vein M_3 lost distad of discal cell. Tergites and sternites mostly blackish-brown.

Description.—*Body coloration:* With extensive dark brown areas, including: clypeus and antennal bases; gena, postgena; labium; antenna (except the scape and pedicel); postpronotal lobe; notum, posterior half of scutellum; anepisternum and katepisternum; anterior and posterior basalares; portion of the anatergite; katatergite; coxae and trochanters (mid coxa less so); hind femora and tibiae; all tergites and sternites.

Head: Antenna with 14 cylindrical segments; pedicel very short. Eye large, completely bare. Palp with 5 segments; basal 2 almost circular, third segment longest and widest; 2 apical segments equal to length of segment 3 but half the thickness. Clypeus protruding, extended to apex of palp segment 3. Labellum large, laterally flattened. Gena, postgena, and labium with numerous, fine, whitish setae. Occiput with 6 stiff, black setae.

Thorax: Notum covered with fine, whitish, decumbent acrostichal setulae. Postpronotal lobe large, with ca. 30 fine, whitish setae. Anepisternum heavily sclerotized, with patch of 20 fine, whitish setae on dorsal lobe; rest of anepisternum bare. Katepisternum completely bare. Anterior and posterior basalare heavily sclerotized. Anepimeron lightly sclerotized, with small patch of ca. 10 fine, whitish setae on postero-dorsal portion. Katatergite sclerotized, bare. Legs: Fore and midlegs yellow, apices of tibiae and tarsi brown. All legs with setulae irregularly arranged (not in longitudinal rows); tibiae and tarsi with 3–4 longitudinal rows of stiff, stout, black setae. Comb on apex of hind tibia not visible: lost with tarsi at surface of amber.

Wings: Membrane with microtrichia only, arranged irregularly, not in rows. Wing veins dark; radial veins darkest. Costal vein

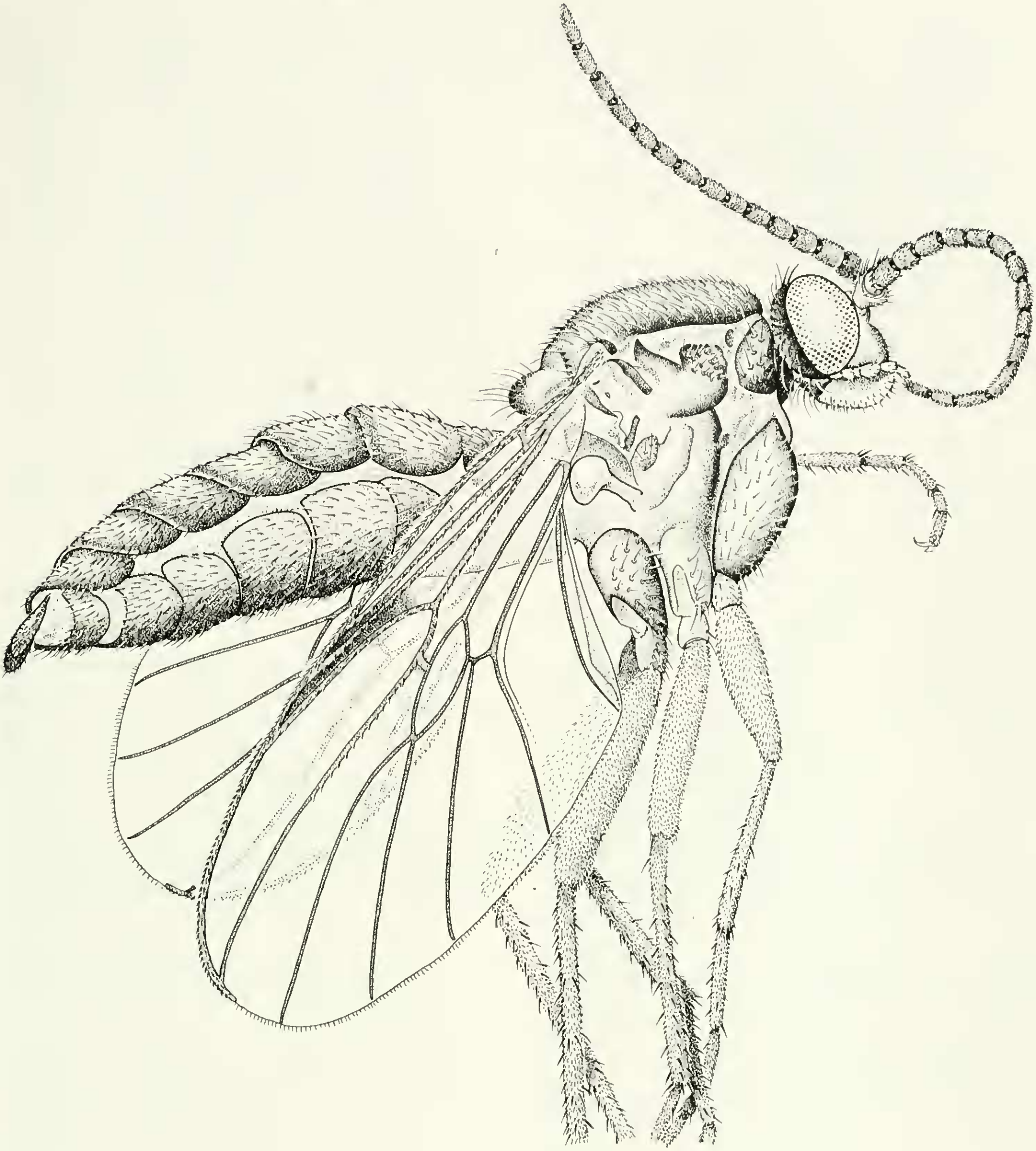


Fig. 1. Habitus of holotype of *Olbiogaster perezi*, n. sp.

extended to slightly past R_{4+5}. Sc and R_1 meeting C very close together. Dark stigmal area surrounding apical half of R_{2+3}. R_{4+5} extended to tip of wing. Crossvein r-m very short, connected to middle of discal cell (d); cell d is fusiform in shape, ends not truncate. Veins M_1 and M_2 arising from apical point of cell d, vein M_3 absent distad of discal cell. Crossvein cu-m very short, proximal to r-m, branch of CuA_1 and CuA_2 almost perpendicular to longitudinal axes of veins. Vein A_1 incomplete, A_2 obscured. Halter light yellow.

Abdomen: Tergites and sternites dark brown; sternites large, covering pleural area. Apical sternite light, elongate, with deep

V-shaped notch in middle. Cerci long, narrow, dark.

Holotype: Female, AMNH-DR11-657, in a clear, light yellow piece of amber, 10 × 13 mm; exact provenance within the Dominican Republic unknown. The surface of the piece on the fly's right side has been ground and polished flat. The specimen is virtually complete, except for loss of the mid and hind tarsi.

Etymology: Patronym, for J. Manuel Perez, an amber dealer in Orlando, Florida, who made this specimen available for study.

RELATIONSHIPS

Tozoni (1989) presented a phylogenetic analysis of the species of *Olbiogaster*, including 21 described and 7 new species (the new species are actually described in Tozoni [1994], with an additional 6 species). Her phylogeny of the genus included four major subgroups widely distributed in the Neotropical region. The genus is defined here in the sense of Amorim and Tozoni (1994), diagnosed above. Features used in her analysis were derived mostly from male terminalia and body coloration. Sexual dimorphism in sclerite colors exists, and not all species are known by both sexes, so separate cladograms had to be developed for males and females. In both males and females there occurred transformation series where the color of sclerites changed from brown to ocher or yellow.

Olbiogaster has most sclerites brown, except part of the scutellum, epimeron II and capitulum of the halter. It is thus clear that *O. perezi* is not a recently derived species in the genus. The basal levels of Tozoni's (1989) phylogeny for the recent species is completely resolved into five clades. Character incongruence was evaluated using the ACCTRAN and DELTRAN procedures, which allowed for reversals and multiple origins of characters, respectively (Figs. 2, 3). The reversals in the cladogram of Fig. 2 do not imply reacquisition of complex structures, so this shorter cladogram is the preferred explanation.

We present below Tozoni's (1989) list of the features that can be examined in the fossil species (e.g. external female), and which refer to the level of generality of this discussion; the character matrix is presented in Table 1. Note that *Olbiogaster mexicana* is known from Mexico, *O. danista* from Dominica, *O. erythrohydra* and *O. tamoioi* are from southeastern Brazil; the remaining species, in the *marinonii* group, occur throughout the Neotropical Region (except Chile and southern Argentina). Plesiomorphic states are given first for each character. Use of a superscript cross ($^+$) denotes a monophyletic group plus its sister group(s). This is a convention established by Amorim and used elsewhere (e.g., Amorim and Tozoni, 1994).

1. Scutum entirely brown/scutum yellow or ochre.

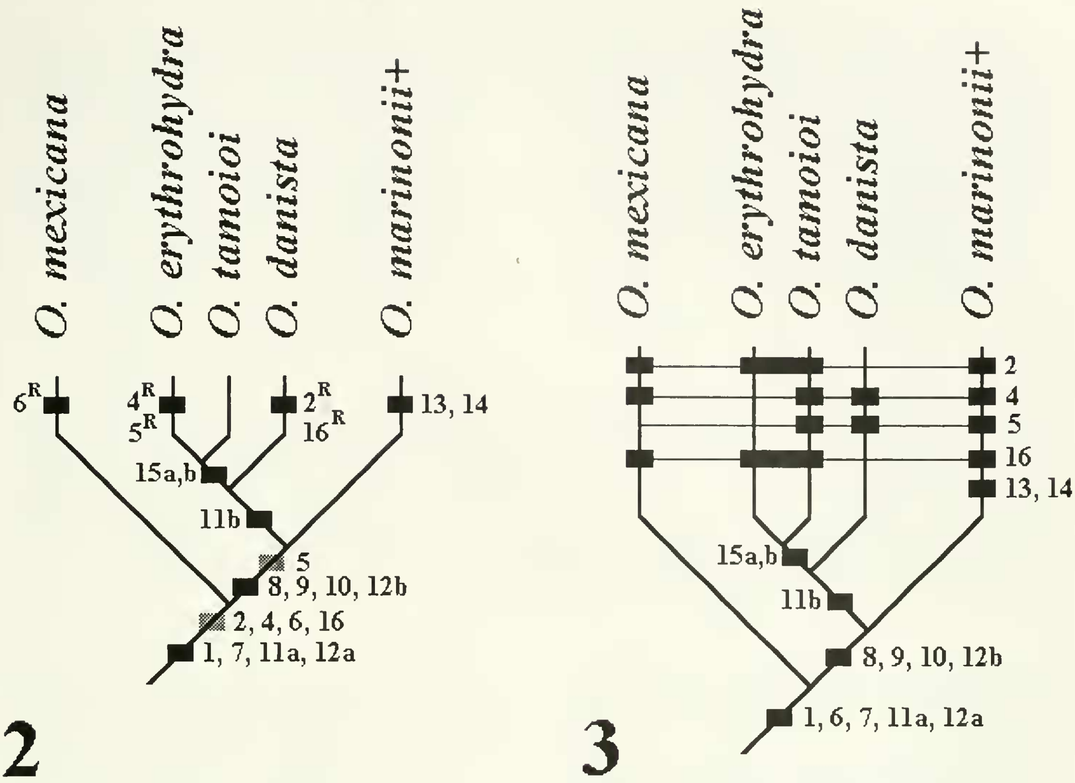
The plesiomorphic condition of this character in *Olbiogaster* is found only in *O. perezi*. This is one of the features that indicates *O. perezi* is the probable sister group of all the remaining species of the genus. Most species of *Eogaster, Austrogaster,* and *Olbiogaster* have a brown scutum, leaving no doubt about the polarity of the character.

2. Scutellum entirely brown/scutellum entirely yellow or ochre.
3. Scutellum entirely brown/scutellum yellow below.

The polarization of these characters is also unquestionable. An entirely brown scutellum is known to occur only in *O. danista*, from Dominica. *Olbiogaster perezi* is plesiomorphic for the color in the dorsal part of the scutellum, but has an apomorphic color for the ventral surface of the scutellum. Character two also indicates that *O. perezi* would be the sister group of the remainder of the genus.

4. Anepisternum entirely brown/anespisternum entirely yellow or ochre.

The plesiomorphic condition of this character is found in *O. perezi* and *O. erythro-*



length = 23 steps

length = 27 steps

Figs. 2, 3. Basal relationships of *Olbiogaster* as proposed by Tozoni (1989), with two interpretations for the transformation series. 2, ACCTRAN procedure for all characters, allowing for character reversals (shaded characters). 3, DELTRAN procedure for all characters, allowing for multiple origins of characters (characters placed above in the cladogram).

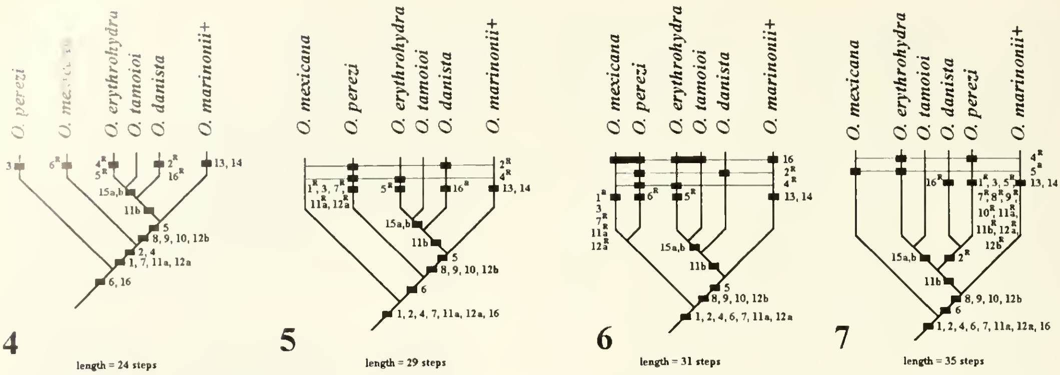
hydra. Some species belonging to the monophyletic *marinonii*$^+$ group have brown maculae on the anepisternum, but character optimization shows that the ground plan of this group should be apomorphic for these characters (species with maculae being cases of reversals). An ACCTRAN optimization of this character results in two steps, a DELTRAN approach produces four. However, neither approach affects the position of *O. perezi* in the cladogram, since the monophyly of *erythrohydra* + *tamoioi* is well supported and unambiguous.

5. Katepisternum brown/katepisternum entirely yellow or ochre.

The plesiomorphic condition of this character is found in *O. perezi,* as well as in *O. mexicana* and *O. erythrohydra.* As in the preceeding character, some species of the *marinonii*$^+$ group also have brown maculae on the katepisternum, but the group is apomorphic in its ground plan. On this basis

Table 1. Character matrix for the basal groups of *Olbiogaster.*

	Character			
		1	11111	1
Taxon	12345	67890	12345	6
Outgroups	00000	00000	00000	0
perezi	00100	10000	00000	1
mexicana	11010	01000	10000	1
erythrohydra	11000	11111	21002	1
tamoioi	11011	11111	21002	1
danista gr.	10011	11111	21000	0
marinonii gr.	11011	11111	11110	1



Figs. 4–7. Four topologies for the relationships of *O. perezi* with remaining species of the genus. 4, Characters 1, 2, 4, 7, 11a, and 12a are taken as true synapomorphies, so *O. perezi* would be the sister group of the rest of the genus. 5, Characters 5, 6, 8, 9, 10, and 12b are considered true synapomorphies, so *O. mexicana* becomes the sister group to the rest of the genus, with *O. perezi* as the next plesiomorphic sister group. 6, Assumption of character 16 having multiple origins and the apomorphic condition shared by *O. perezi* and *mexicana* interpreted as a true synapomorphy. 7, Reversal of character 2 interpreted as a true synapomorphy, which links *danista* and *perezi*, and many plesiomorphic conditions in the latter species thus becoming reversals.

the fossil species is excluded from the *marinonii*$^+$ group.

6. Epimeron II entirely yellow/epimeron II entirely brown.

Olbiogaster perezi has epimeron II entirely yellow (sometimes referred to in the Anisopodidae as the anepimeron). *Olbiogaster mexicana,* on the other hand, has the sclerite entirely brown (based on the published description) and some species of the *marinonii*$^+$ group also have epimeron II maculated brown. The fact that *O. perezi* shares the apomorphic condition with the remaining species of the genus except *O. mexicana* indicates that it could belong to the *danista*$^{++}$ group (Figs. 5–7), a topology different from that suggested by characters 1, 2, 4, 7, and 12a (Figs. 4–6).

7. Mediotergite entirely brown/mediotergite entirely yellow or ochre.

Olbiogaster perezi is the only species in the genus to have the mediotergite entirely brown. This would indicate a sister-group relationship between *O. perezi* and the rest of the genus.

8. Coxa I entirely brown/coxa I entirely yellow or ochre.
9. Coxa II entirely brown/coxa II entirely yellow or ochre.
10. Coxa III entirely brown/coxa III entirely yellow or ochre.

Olbiogaster mexicana is the only species of the genus sharing with *O. perezi* the plesiomorphic condition of this character. Although the two species cannot be linked on the basis of this symplesiomorphy, it corroborates that *O. perezi* does not belong to the *danista* group.

11. Femur III entirely brown/a. with distal ¼ brown / b. entirely yellow or ochre.

The presence of an entirely brown femur III in *Olbiogaster* is exclusive to *O. perezi.* At this level of the analysis, the most apomorphic condition, of femur III being entirely yellow, is found only in the species of the *danista*$^+$ group, and occuring homoplasiously in the *marinonii*$^+$ group. The first step corroborates the hypothesis of *O. perezi* being the sister group to the remaining *Olbiogaster.*

12. Tergites I–IV entirely brown/a. with distal ⅕ yellow / b. with distal ½ yellow.
13. Tergites I–IV entirely brown/with a median yellow line on distal ⅔.
14. Tergites I–IV entirely brown/a. with a yellow band laterally on distal ⅔. / b. with a complete yellow band.
15. Tergite V entirely brown/with a median yellow line on distal ⅔.

A complex transformation series is proposed by Tozoni (1989) for the coloration of the abdominal tergites in *Olbiogaster*, varying from brown to yellow. These modifications include independent changes in different areas of the sclerite (distally, laterally, and mesally), and with homoplasious origins of some of these changes. *Olbiogaster perezi* is the only known species with the tergites entirely brown. *Olbiogaster mexicana* has only the distal fifth of tergites I–IV yellow and other species have a larger portion of the tergites yellow. This, once more, confirms the basal position of *O. perezi* in the genus.

16. Capitulum of halter brown/yellow.

Olbiogaster has the capitulum yellow, as do other basal species of the genus with the exception of the *O. danista* and some species belonging to the *marinonii*$^+$ group. If the apomorphic condition of the character is attributed to the ground plan of the genus, the plesiomorphic condition of this character in *O. danista* would be a reversal.

Of the list above, *O. perezi* is apomorphic only for characters 3, 6, and 16. Character 3 is an autapomorphy. Character 6 is shared with all *Olbiogaster* except *O. mexicana* and character 16 is shared with most species of the genus, but is plesiomorphic in *O. danista*. The plesiomorphic conditions of characters 13 and 14 exclude *O. perezi* from the *marinonii* group. The topology of the most parsimonious cladogram has *O. perezi* as the sister group of all remaining known recent *Olbiogaster* (Fig. 4). The apomorphic features of *O. perezi*, however, allow for some alternative hypotheses. *Olbiogaster perezi* could be the sister group of all recent species of the genus except *O. mexicana*, which in this case would be the most basal species of the genus (Fig. 5). This hypothesis would be obtained if we consider the yellow epimeron II of *O. perezi* (character 6) homologous to the same feature seen in other species of the genus. *Olbiogaster perezi* is theoretically the sister species of *O. mexicana*, if we consider the yellow halter capitulum to be homologous among them (Fig. 6). Finally, *O. perezi* could be the sister group of *O. danista* if we accept character 6 as having a single origin in the group and the brown scutellum (character 2) of *O. perezi* and *O. danista* being homologous (Fig. 7). Still other topologies present even less parsimonious character evolution. The length of the cladogram in which *O. perezi* is the sister group to the remaining species of the genus has 24 steps, five steps shorter than the second most parsimonious cladogram. The other two cladograms have 32 and 35 steps, respectively.

A sister-group relationship of *Olbiogaster perezi* to the other species of the genus adds a basal stem to this monophyletic group. The autapomorphies shown by *O. perezi*—particularly the virtual absence of vein M_3—indicate that the fossil is itself a derived clade arising mostly closely from the stem group, but not an ancestral member of the genus.

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